HELMINTHS OF SOCKEYE SALMON (*ONCORHYNCHUS NERKA*) FROM THE KVICHAK RIVER SYSTEM, BRISTOL BAY, ALASKA[1]

DAVID A. PENNELL,[2] C. DALE BECKER,[3] AND NORA R. SCOFIELD[4]

ABSTRACT

A study of helminths infecting juvenile and adult sockeye salmon (*Oncorhynchus nerka*) leaving and entering the Kvichak River system, Bristol Bay, Alaska, was conducted in 1969. Ten helminths acquired in fresh water were found in smolts: *Diplostomulum* sp.; an unidentified trematode; *Diphyllobothrium* spp.; *Triaenophorus crassus* Forel, 1868; *Proteocephalus* sp.; *Eubothrium salvelini* (Schrank, 1790); *Neoechinorhynchus rutili* (Mueller, 1789); *Philonema oncorhynchi* Kuitunen-Ekbaum, 1933; *Rhabdochona* sp.; and *Contracaecum* sp. In addition to surviving larval stages of freshwater parasites, adults were infected by nine helminths acquired in the sea: *Gyrodactyloides strelkowi* Bykhovskaya and Polyanskaya, 1953; *Lecithaster gibbosus* (Rud., 1802); *Brachyphallus crenatus* (Rud., 1802); *Tubulovesicula lindbergi* (Layman, 1930); *Phyllobothrium caudatum* (Zschokke and Heitz, 1914); *Echinorhynchus gadi* Mueller, 1776; *Bolbosoma caenoforme* Heitz, 1920; *Anisakis* sp.; and *Contracaecum* sp. Infection incidences and intensities are tabulated where accurate data are available. Information on life histories is assembled from scattered sources, and some ecological aspects of helminths infecting Kvichak sockeye salmon are briefly discussed.

The Kvichak River system is the largest producer of sockeye salmon, *Oncorhynchus nerka* (Walbaum), among five river systems in Bristol Bay, western Alaska. Its drainage basin covers nearly 8,000 square miles and includes two large lakes, Iliamna Lake (90 miles long and up to 26 miles wide) and Lake Clark (50 miles long and up to 4 miles wide). Intensive studies on sockeye salmon from this system and the other four systems, the Wood River, Naknek River, Egegik River, and Ugashik River, have been underway since 1946 (Thompson, 1962). Recent research has been directed toward determining the biological basis for annual fluctuations in the number of seaward migrants and subsequent return of adults 2 and 3 years later, and providing a reliable estimate of the optimum escapement for each of these river systems (Burgner et al., 1969).

The survival rate for Kvichak River sockeye salmon is generally higher in the peak year of the abundance cycle than in other years since the total production from each year class comes in installments 4, 5, or 6 years later, depending on the total age of the adults when they return to spawn. The occurrence of mortality inversely related to density has been ascertained from observations, but its causes remain unidentified. Since the available records show that, generally, smolt production has been proportionate to adult escapement, it appears that losses occur primarily after the smolts leave the nursery areas, but the possibility remains that the predisposing conditions are found in fresh water. The adjustments that smolts make to environmental changes, their physiological condition, and their resistance to stress have been studied by those who seek the factors that underlie variations in survival rate among year classes in

[1] This study was supported by funds provided by the Washington Sea Grant Program, which is maintained by the National Oceanic and Atmospheric Administration of the U.S. Department of Commerce. Contribution No. 369, College of Fisheries, University of Washington.

[2] Fisheries Research Institute, College of Fisheries, University of Washington, Seattle, WA 98105; now deceased.

[3] Ecosystems Department, Battelle Memorial Institute, Pacific Northwest Laboratories, Richland, WA 99352.

[4] Fisheries Research Institute, College of Fisheries, University of Washington, Seattle, WA 98105; present address: University of Idaho, Moscow, Idaho 83843.

Manuscript accepted January 1972.
FISHERY BULLETIN: VOL. 71, NO. 1, 1973.

the sea. Parasitic infections are considered a possible factor; albeit their effects may be largely sublethal, nevertheless they might contribute to disproportionate survival rates.

A field study of the helminth fauna of sockeye salmon in the Kvichak system was commenced in 1968 and expanded in 1969. The immediate tasks were to (1) identify the parasites acquired in fresh water and those acquired in the sea, (2) determine the incidence and intensity of infections, and (3) review the available literature for information on life cycles. Earlier studies by Margolis (1963) concentrated on parasites of sockeye salmon in the North Pacific Ocean as biological indicators of continental origin; he noted that over 50 parasitic species of freshwater and marine origin are known to infect sockeye salmon occurring in the North Pacific Ocean and adjacent seas. Many of these parasites occur in other species of salmon that come from Eurasia and North America to feed and mature in these waters (Akhmerov, 1963; Mamaev, et al., 1959; Mamaev and Oshmarin, 1963; Zhukov, 1960).

MATERIALS AND METHODS

The Kvichak River system consists of Iliamna Lake and Lake Clark, their tributaries, and the Kvichak River, which leads to the sea (Figure 1). Smolts migrate seaward for a few weeks following ice breakup in late May, whereas adults return to spawning grounds in July. Samples were taken from four groups of fish in 1969 (Figure 1): 1) smolts, captured by fyke net at Igiugig, on the Kvichak River (Site I), between May 28 and June 6; 2) adults in Bristol Bay, collected by set nets at Pederson Point (Site II) during May; 3) adults in fresh water, taken by beach seine in the Newhalen River (Site III) during mid-July; and 4) spawners, collected by beach seine on spawning grounds at Finger Beach (Site IV), Woody Island (Site V), and Porcupine Island (Site VI) during August. No attempt was made to discriminate between smolts originating from Iliamna Lake and Lake Clark. Adults collected at Pederson Point in Bristol Bay were known from past tagging experiments to consist almost entirely of Kvichak sockeye.

The skin, gills, eyes, gastrointestinal tract, viscera, body cavity, and swim bladder of the fish were examined for helminths. Blood smears were prepared from each fish, gall bladder smears were made from adults, and brain tissue imprints were taken from smolts. Examinations were usually conducted on the day of capture. Thus, most helminths were recovered, tentatively identified, and counted while alive and before preservation in hot Formalin[5]-Acetic acid-Alcohol solution (standard solution). In some cases tissues were preserved in hot Bouin's solution (standard solution) for future dissection and examination for parasites. Representative specimens of cestodes and trematodes were stained in Delafield's hematoxylin and mounted for further study; nematodes were either stained

[5] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

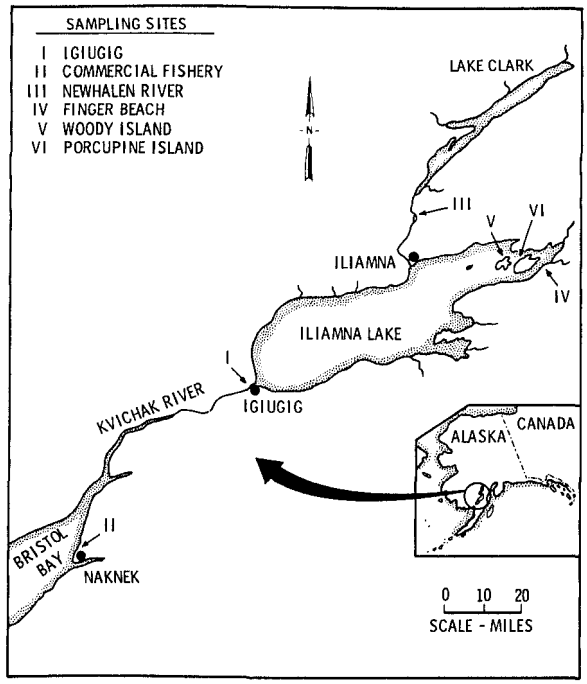

FIGURE 1.—Map of the Kvichak River system, showing sampling sites, with inset map showing its location in southwestern Alaska.

with methyl blue-lactic acid or cleared unstained in lactic acid, and examined unmounted. Blood and tissue smears were air dried, fixed in absolute methyl alcohol, and treated with Wright's blood stain.

In this report incidence and intensity are used to describe the percentage of infected hosts and the average number of parasites per infected fish, respectively. Incidences and intensities were determined with confidence for the relatively small smolts, but only the incidences were judged to be reliable for the adult fish because of difficulty in obtaining accurate counts of frequently abundant helminths.

To accurately determine the age of the host, scales from smolts and otoliths from adults were preserved and read for age, and the readings were checked against the recorded length of the fish. The smolts were from the 1966 and 1967 brood years and were designated as age 2 and age 1 according to the number of winters spent in fresh water. The adults were from the 1963, 1964, and 1965 brood years and had spent either two or three winters in the sea.

RESULTS AND DISCUSSION

Parasitological examinations were completed on 212 smolts, 88 adults from Bristol Bay, and 71 adults from fresh water. The identities and incidences of helminths in these fish are shown in Table 1 under appropriate area and age designations. No haematozoa, myxosporidians, microsporidians, leeches, or copepods were

TABLE 1.—Incidence of helminths in young and adult sockeye salmon from the Kvichak River system in 1969. (Incidence in parentheses as a percentage.)

Parasite[1]	Smolts[2]		Adults[2]						
	Kvichak River		Bristol Bay			Newhalen River		Spawning grounds	
	1.	2.	1.2	2.2	1.3 + 2.3	1.2	2.2	1.2	2.2 + 1.3
Number of fish sampled	60	152	32	46	10	33	2	26	10
Monogenea									
Gyrodactyloides strelkowi Bykhovskaya and Polyanskaya, 1953	0	0	1(3)	4(9)	1(10)	0	0	0	0
Digenea									
**Diplostomulum* sp. (spp?)	36(60)	102(67)	5(16)	7(15)	0	10(30)	2(100)	13(50)	2(20)
Lecithaster gibbosus (Rud., 1802)	0	0	29(91)	46(100)	10(100)	31(94)	1(50)	23(88)	7(70)
Brachyphallus crenatus (Rud, 1802)	0	0	3(9)	3(7)	0	3(10)	0	4(15)	1(10)
Tubulovesicula lindbergi (Layman, 1930)	0	0	0	0	0	2(6)	0	1(4)	0
Unidentified Digenea	0	2(1)	0	0	0	0	0	0	0
Cestoda									
**Diphyllobothrium* spp.	21(35)	100(66)	3(9)	6(13)	1(10)	0	0	0	0
**Triaenophorus crassus* Forel, 1868	0	4(3)	0	0	0	0	0	0	0
***Proteocephalus* sp. (spp?)	37(62)	72(47)	0	0	0	0	0	0	0
Eubothrium salvelini (Schrank, 1790)	1(2)	2(1)	0	0	0	0	0	0	0
***Phyllobothrium caudatum* (Zschokke and Heitz, 1914)	0	0	32(100)	46(100)	10(100)	33(100)	2(100)	26(100)	10(100)
Acanthocephala									
Neoechinorhynchus rutili (Mueller, 1780)	1(2)	20(13)	0	0	0	0	0	0	0
Echinorhynchus gadi (Mueller, 1776)	0	0	0	4(9)	2(20)	1(3)	0	0	0
***Bolbosoma caenoforme* Heitz, 1920	0	0	22(69)	34(74)	6(60)	4(12)	0	7(27)	1(10)
Nematoda[3]									
Philonema oncorhynchi Kuitunen-Ekbaum, 1933[4, 5]	60(100)	140(92)	23(72)	38(83)	7(70)	32(97)	2(100)	26(100)	9(90)
Rhabdochona sp.	0	8(5)	0	0	0	0	0	0	0
Anisakis sp. (spp.?)[5]	0	0	--	--	--	--	--	--	--
Contracaecum sp. (spp.?)[5]	1(2)	18(12)	--	--	--	--	--	--	--
*Other nematodes[6]	--	--	31(97)	45(98)	10(100)	33(100)	2(100)	20(77)	9(90)

[1] * = larvae (in fish intermediate host), ** = postlarvae (sexually undeveloped parasite).
[2] Age designation is based on Arabic numerals corresponding to the number of winters lived. Freshwater age precedes the dot, salt water age follows the dot; i.e., 2.2 = adult, 2 winters in fresh water, 2 winters in the sea.
[3] Examination of adult sockeye for nematodes was restricted to the digestive tract, viscera and body cavity.
[4] Incidence of P. *oncorhynchi* in smolts was based on larvae in the swim bladder; in adults, on encystation of mature worms among the viscera and on body cavity wall.
[5] Of nematodes preserved from Bristol Bay adult sockeye, the ratio (in total numbers) of *P. oncorhynchi* to *Anisakis* to *Contracaecum* was about 1:2:1.5.
[6] Primarily *Anisakis* and *Contracaecum* in Bristol Bay adult sockeye, primarily *Anisakis* in adults reaching fresh water.

detected. Some of the genera of helminths may be represented, in fact, by more than one species since specific identification of some immature forms was not possible. The parasites are considered under five taxonomic groups: Monogenea, Digenea, Cestoda, Acanthocephala, and Nematoda. Some data on the life cycle of each parasite, which are essential to an understanding of the cause-and-effect relationships for parasitic infections, are given where available.

MONOGENEA

No monogenetic trematodes of freshwater origin were found on the gills of smolts, although *Tetraonchus alaskensis* Price, 1937 has been reported from young sockeye salmon in the Wood River system (Margolis, 1963, tables). *Gyrodactyloides strelkowi* (Gyrodactylidae) parasitized the gills of five adults taken at Pederson Point. This viviparid is specifically a salmon parasite (Margolis, 1965) and is phylogenetically related to the genus *Gyrodactylus* which parasitizes primarily freshwater teleosts. Since *G. strelkowi* lives externally on its host and is adapted only to marine conditions, it is lost soon after the return of adult sockeye salmon to fresh water.

DIGENEA

Two species of dignetic trematodes were acquired by smolts in fresh water, and three species by maturing fish in the sea.

Metacercariae of the trematode genus *Diplostomulum* (Diplostomatidae) occurred in the eye lenses of over half of the smolts. The incidence of infection was slightly less in age 1 (60%) than in age 2 smolts (67%). Infection normally occurs via furcocercous cercariae that emerge from freshwater gastropods, penetrate the skin of various fish, and localize in their eyes as metacercariae. Studies on *Diplostomum spathaceum* (Rud., 1819), a widely distributed Palearctic species that matures in the intestine of gulls, indicate that infection of fish does not occur in brackish water, a result of the absence of required freshwater molluscan hosts (Cichowlas, 1961). The incidence of *Diplostomulum* in returning adults taken at Pederson Point was significantly lower (15-16%) than in departing smolts, but still less than in adults penetrating into the headwaters of the Kvichak; thus those fish that returned to spawn were again exposed to cercariae after re-entry.

Variable numbers of three hemiurid trematodes were found in the stomach and upper intestine of adult sockeye salmon from Bristol Bay: *Lecithaster gibbosus, Branchyphallus crenatus,* and *Tubulovesicula lindbergi* (Hemiuridae). All were acquired in the marine environs by ingestion of crustacean plankters that serve as second intermediate hosts and carry the stages maturing in sockeye salmon. The incidence of *L. gibbosus* in sockeye salmon at Pederson Point exceeded 90% and was only slightly less in adults collected from the spawning grounds. Margolis (1963) noted that the rate of infection by *L. gibbosus* in sockeye salmon was lower in offshore than in inshore areas and deduced that most parasites in maturing fish were acquired after they re-entered coastal waters. This conclusion was supported by data of Mamaev and Oshmarin (1963) for sockeye salmon taken along the Soviet eastern coast and of Boyce (1969) for those from British Columbia waters. The acquisition of the parasites in coastal areas is presumably related to the relatively high abundance of molluscan first intermediate hosts. Boyce (1969) found that marine snails of the genus *Thais* were the first intermediate host and the marine copepods *Centropages abdominalis* and *Pseudocalanus minutus* were the second intermediate hosts of *L. gibbosus* in coastal areas of British Columbia. *L. gibbosus* matures in 1 to 2 weeks and has a lifespan of about 2 to 9 months in pink salmon, whereas *Tubulovesicula lindbergi* matures in 2 to 4 months and lives at least 31 months in chum salmon (Margolis and Boyce, 1969). Thus most trematodes acquired in coastal waters and maintained in the digestive tract of sockeye salmon during their migration into the Kvichak system are likely to persist until their post-spawning death.

Branchyphallus and *Tubulovesicula* were of comparatively low incidence, and *Hemiurus levinseni* Odhner, 1905, a marine hemiurid known to infect adult salmon in the North Pacific, was

not found. The distribution of these parasites appears to be somewhat sporadic. Data tabulated by Margolis (1963) from Bristol Bay sockeye salmon in 1957 suggest that *B. crenatus* is more common (40% incidence) in Kvichak fish than our samples indicate, but concur on the relative scarcity of *T. lindbergi* and absence of *H. levinseni*.

CESTODA

The tapeworms belonged to five genera and, with the exception of *Eubothrium*, were either plerocercoid larvae, encysted among the viscera, or sexually immature, postlarval forms in the intestinal lumen. Presumably all infections were acquired by ingestion of cyclopid and/or diaptomid copepods containing infective procercoids.

Encysted plerocercoids belonging to the genus *Diphyllobothrium* (Diphyllobothriidae) were fairly common in the stomach walls of many smolts but also occurred, though less frequently, in the liver, spleen, and the intestinal wall. Since the incidence of infection was higher in smolts of age 2 (66%) than in those of age 1 (35%), it appears that the plerocercoids accumulate with continued sojourn of the fish in the lake environment. The incidence of *Diphyllobothrium* larvae in the viscera of adult sockeye salmon from Pederson Point, which had spent 2 or 3 years in the sea, was significantly lower (9-13%). Diphyllobothriasis is common in freshwater salmonids of the Northern Hemisphere (Becker and Brunson, 1967), but the identities and life cycles of many forms remain unclear. Vik (1964) reviewed the bionomics of *Diphyllobothrium*, and Stunkard (1965) and Meyer (1966) discussed taxonomic problems. Rausch (1954) described the plerocercoids of *D. ursi* Rausch, 1954, from juvenile and adult sockeye salmon and the adult cestodes from bears on Kodiak Island, Alaska. Rausch and Hilliard (1970) identified six species of *Diphyllobothrium* indigenous in Alaska and noted that several occur as plerocercoids in salmonids and other freshwater fishes. In all probability, the plerocercoids present in Kvichak sockeye salmon represent two or more species with different definitive hosts (birds or mammals) but with otherwise similar life cycles.

Larvae of *Triaenophorus crassus* (Triaenophoridae) were encysted in either the body cavity or muscle of only four smolts, all of which were age 2. None was detected in returning adults, although apparently the plerocercoids can survive in ocean-dwelling salmon for 4 or 5 years (Margolis, 1963). This cestode is specific for its definitive host, the northern pike (*Esox lucius*); however, the first intermediate host may be one of several species of freshwater copepods (Watson and Lawler, 1965), and the second is a planktivorous fish. Reviews of *T. crassus* and other species of *Triaenophorus* were made by Miller (1952), Lawler and Scott (1954), and Michajlow (1962). In the Kvichak system, the incidence of *T. crassus* in sockeye salmon smolts is apparently low, but it varies among other river systems bordering Bristol Bay (Margolis, 1963, 1967). The fact that Kvichak smolts are largely pelagic apparently accounts, in part, for the low incidence of infection by *T. crassus*, since copepods infected with procercoids will occur most abundantly in shallow, marshy inshore areas inhabited by pike. (Field observations by the second author in 1958 indicated that the incidence of *T. crassus* plerocercoids was higher in smolts from Lake Clark, which has a comparatively greater proportion of shoreline to water mass, than in those from Iliamna Lake.)

Tiny postlarvae of *Proteocephalus* sp. (Proteocephalidae) occurred in the intestinal lumen of about half of the Kvichak smolts, but the incidence of infection was lower in age 2 fish (47%) than in age 1 (62%). Presumably these cestodes had recently emerged after infected copepods were ingested and the smolts were fortuitous hosts in which further development was restricted. The larvae of *Proteocephalus* in age 2 smolts were no further advanced than those in age 1, and the incidence of infection was lower (47 versus 62%); thus it appears that these cestodes soon perish. No *Proteocephalus* occurred in returning adult sockeye. The favored definitive hosts of this parasite probably are resident fish in the Kvichak system.

Eubothrium sp. (Amphicotylidae), probably *E. salvelini* Schrank, 1790) on ecological

grounds, occurred as adults in the intestines of three smolts. This holarctic cestode appears to be rare in sockeye salmon in major Bristol Bay watersheds (Margolis, 1963, tables) but is sometimes common in salmonids from other areas. Infections of about 35% incidence occurred in sockeye smolts leaving Babine Lake, British Columbia, in 1952 and 1953 (Dombroski, 1955), and an incidence of 20-30% among these migrants has been recorded recently (Smith and Margolis, 1970). There is no teleost intermediate host for *Eubothrium,* and juvenile sockeye salmon become infected directly by ingestion of planktonic copepods carrying procercoids, such as *Cyclops strenuus* in Norway (Vik, 1963). *E. salvelini* apparently does not survive the sojourn of growing sockeye salmon at sea. Recent evidence suggests that cestodes of a related species, *Eubothrium crassum* (Bloch, 1779), found in returning Atlantic and Pacific salmon in rivers, are rarely the same worms carried to sea by smolts but are of marine origin, and that two biological races, one marine and one fresh water, exist (Kennedy, 1969).

Postlarval forms of *Phyllobothrium caudatum* (Tetraphyllidea) were found in the digestive tract of all fish taken at Pederson Point, the Newhalen River, and the spawning grounds (mean intensity, 16/fish). Little decrease was apparent in either incidence or intensity of infection in adults that reached fresh water despite their cessation of feeding. The unencysted postlarvae exist in a state of arrested development. They live in captive juvenile pink and chum salmon in seawater for at least 8 months with no change in form, but grow from 1 to 4 or 5 mm (Boyce, 1969). Moderate to heavy infections of phyllobothriids are acquired by nearly all species of salmon feeding in the North Pacific (Akhmerov, 1963; Margolis, 1963; Zhukov, 1960) and their numbers are apparently cumulative. The mature form and the definitive host of this cestode remain unknown, and some taxonomic confusion exists as to its specific identity. Williams (1968), who reviewed the Phyllobothriidae, concurred with Margolis (1963) in identifying the postlarvae from sockeye salmon in the North Pacific and adjacent seas as *P. caudatum.* The hosts of larval *Phyllobothrium* include marine cephalopods, elasmobranchs, teleosts, and mammals, but the mode of infection and subsequent behavior of the late procercoid and developing plerocercoid are not known (Williams, 1968).

ACANTHOCEPHALA

The incidence of *Neoechinorhynchus rutili* (Neoechinorhynchidae) among the smolts was low and tended to be greater among those of age 2 (13%) than those of age 1 (2%). None was found in returning adult sockeye. Tabulated data by Margolis (1963) indicate that this acanthocephalan does not survive the sockeye's ocean residence. *N. rutili* developed rapidly, and hence the parasites carried in the intestine of smolts were sexually mature. Margolis (1963) listed an incidence of 8% in Kvichak smolts examined in 1956.

N. rutili is an euryxenous parasite with wide dispersal in freshwater habitats of Eurasia and North America (Van Cleave and Lynch, 1950) and is the only species of the genus found in European freshwater fishes (Bullock, 1970). The only known intermediate host of *N. rutili* in North America is the ostracod *Cypria turneri* (Merritt and Pratt, 1964), whereas in Great Britain there are two known intermediate hosts, the ostracods *Cypria ophthalmica* and *Candona candida* (Walker, 1967). The ostracod *Cyclocypris laevis* and two species of *Sialis* (Insecta) are known to transmit the infective larvae to fish in Europe (Ginetsinskaya, 1958).

Echinorhynchus gadi (Echinorhynchidae) occurred in six adult sockeye salmon from Pederson Point. According to Margolis (1965), this acanthocephalan is widely distributed in northern seas; it is common in sockeye salmon taken off the Kamchatka Peninsula of the USSR but is generally rare in salmon captured in other areas, including the North American coast. *E. gadi,* like *N. rutili,* is an euryxenous parasite but differs in that it originates in the sea. It occurs in many families and genera of teleosts in the North Pacific and North Atlantic, particularly demersal fishes, but most commonly in the cods (Gadidae) (Linton, 1933; Margolis, 1965; Sindermann, 1966). The first intermediate hosts are marine amphipods, such as *Gammarus lo-*

custa, Amphithoe rubricata, and *Pontoporeia femorata* in European waters (Ginetsinskaya, 1958) and *Cyphocaris challengeri* off the coast of British Columbia (Ekbaum, 1938). Infections are gradually lost because of the relatively short lifespan of the mature parasite when anadromous salmon cease feeding (Ginetsinskaya, 1958).

Postlarval forms of *Bolbosoma* sp. (Polymorphidae), probably *B. caenoforme* on ecological grounds, were common in the intestine of adult sockeye salmon from Pederson Point (60-74% incidence), but the incidence decreased over a 3-month period as the fish penetrated into fresh water. The decrease in incidence was accompanied by a decrease in mean intensity from about 5 (range, 1-15) in fish taken from Bristol Bay to about 2 (1-6) in fish collected on the spawning grounds. Maturation of *B. caenoforme* appears to be inhibited in salmon, which are presumably accidental hosts. The definitive hosts are believed to be marine mammals. Nevertheless, there is a wide distribution and high incidence of this acanthocephalan in salmon feeding in waters of the North Pacific (Akhmerov, 1963; Mamaev et al., 1959; Margolis, 1963, table).

Four species of juvenile *Corynosoma* (Polymorphidae) were reported in sockeye salmon from the North Pacific and adjacent seas by Margolis (1958), but the incidence was less than 2%. One species, *C. villosum* Van Cleave, 1953, was reported in Ugashik River sockeye salmon in 1957 but not in other Bristol Bay adults (Margolis, 1963, table). No *Corynosoma* were found in Kvichak adult sockeye salmon during this study.

NEMATODA

Philonema oncorhynchi (Philometridae) was the common nematode parasitizing the smolts, but the incidence from our data was higher in age 1 (100%) than in age 2 (92%). Larval forms commonly occurred in the swim bladder, occasionally in the kidney, and rarely in other visceral organs. The larvae apparently leave the swim bladder or tissues during the sockeye salmon's sojourn at sea and enter the body cavity, where they mature in synchrony with maturation of the host (Margolis, 1970). In the adults taken at Pederson Point, the incidence of *P. oncorhynchi* exceeded 70%, and the mature worms were localized in the body cavity. Data tabulated by Margolis (1963) indicate that the incidence of this nematode in sockeye salmon returning to major Bristol Bay tributaries is generally high (92 - 100%) and that the intensity of the infections is relatively high (averaging 11-61 parasites/fish). There is little doubt that the very small nematodes reported in sockeye salmon smolts leaving Bristol Bay tributaries in 1956 (100% incidence) by Margolis (1963) were, as he assumed, larvae of *P. oncorhynchi.*

Recent data have elucidated the life cycle of this dracunculoid nematode, which infects salmonids in fresh water on both borders of the North Pacific Ocean. Gravid worms are presumably discharged along with eggs when the adult fish spawn, the worms burst to liberate thousands of larvae, and the larvae are ingested by a suitable copepod intermediate host, such as *Cyclops bicuspidatus* (Platzer and Adams, 1967). Invasive larvae are liberated from infected copepods in the stomach of sockeye smolts, penetrate the gut wall, and move through either the coelomic cavity or the mesentery and associated tissues to the swim bladder within 18 hr (Adams, 1969). Numbers of larvae carried by smolts moving seaward may reach the hundreds (Margolis, 1970), since the intensity of infection tends to increase during the freshwater life of the planktivorous smolts.

Two other nematodes were acquired by the smolts, *Rhabdochona* sp. and *Contracaecum* sp. *Rhabdochona* (Rhabdochonidae) occurred in the intestine of a few age 2 smolts (5%) but not in adult sockeye salmon taken at Pederson Point. Although little is known of the bionomics of various species of *Rhabdochona,* these nematodes are common in various North American freshwater fishes (Choquette, 1951). The incidence of *Contracaecum* was also low in age 1 (2%) and age 2 (12%) smolts, and about one immature nematode was found encysted in the viscera of each infected fish.

Contracaecum and *Anisakis* (Heterocheilidae) are cosmopolitan parasites of many marine fish-

es. Anadromous salmonids carry the parasites into fresh water. Nearly all adult sockeye salmon taken at Pederson Point harbored quantities of larval anisakids belonging to these two related genera. Accurate records of adults infected with either *Contracaecum* and/or *Anisakis* were not obtained, but the actual combined incidence was probably 100%, as tabulated for Bristol Bay sockeye salmon returning in 1957 by Margolis (1963). In our study, these helminths were listed simply as nematodes because of the difficulty of individually examining large numbers of parasites scattered throughout the viscera of the large fish. On the basis of preserved material from adult sockeye salmon taken at Pederson Point, the ratio of *P. oncorhynchi* to *Anisakis* to *Contracaecum* was about 1:2:1.5 by total numbers.

According to Margolis (1970), the typical life cycle of nematodes belonging to the superfamily Ascaridoidea (including all anisakids) occurring in fishes probably involves three hosts—a crustacean or other invertebrate as first intermediate host, a fish as second intermediate host, and a piscivorous fish, bird, or mammal as the definitive host—depending on the genus or species concerned. Whether the larval *Contracaecum* found in Kvichak smolts in this study are identical with those in returning adult sockeye salmon is problematical, but it is possible that stages liberated from spawning fish were acquired by some smolts.

INTENSITIES OF FRESHWATER HELMINTHS IN SMOLTS

Ten helminths with life cycles involving initial transfers in the freshwater environs were harbored by migrating Kvichak smolts (Table 1). One of the objectives of this study was a determination of the potential effects of these helminths, however subtle and indirect they may be. Some indication is provided by the intensity of infections in correlation with the site selected for latent or active development.

Ecologically speaking, the intensity of infection is roughly correlated with the incidence of infection because the more abundant the parasite, the greater will be the distribution of infections among all available hosts. Moreover, the higher the incidence and/or intensity of infection, the more favorable will be the sum of all synecological factors involved in sustaining a particular host-parasite association.

The intensities of the five common helminths acquired by smolts in Iliamna Lake and Lake Clark are given in Table 2. Accurate counts were not made of the ubiquitous *Philonema oncorhynchi* and data on the adventitious *Proteocephalus* sp. are omitted. Some additional data are included from smolts captured in previous years, preserved in Formalin, and subsequently examined. Of these helminths four occurred as immature or larval forms in the body cavity, tissues, or organs.

The acanthocephalan *Neoechinorhynchus rutili* inhabits only the intestine of smolts, where it rapidly matures. In this favored location the female releases the eggs, these are passed externally, and the worms eventually degenerate. Infection burdens were found to be low in this study, with usually one but sometimes two parasites per host. With such low intensities, fertilization of eggs in the intestine (which requires association of a male and a female) is exceptional and the parasite tends to be self-limiting. Consequently, the principal definitive hosts in the Kvichak system are probably resident fishes that sustain an infection foci. The data, though scanty, suggest that infection of smolts occurs primarily in Iliamna Lake since samples from Lake Clark and its tributary, the Newhalem River, harbored none. Data presented by Margolis (1963) for 25 Kvichak smolts in 1956 list an incidence of 8% and a mean intensity of one parasite per fish.

Diplostomulum sp., *Diphyllobothrium* spp., and *Triaenophorus crassus* persist in sockeye salmon as larvae throughout the life of their host. Completion of their life cycles requires that an infected fish be eaten by a predator or scavenger in which the parasite is able to mature and shed its eggs. *Philonema oncorhynchi* transforms from larvae to adult in sockeye and is liberated during the spawning act or upon the host's death.

Both the incidence and intensity of *Triaenophorus crassus* were low in Kvichak smolts in this

TABLE 2.—Incidence and intensity of some helminths from juvenile sockeye salmon in the Kvichak River system in 1961, 1966, 1968, and 1969. (Incidence is the percentage of the sample infected; mean intensity, from infected fish only, in parentheses.)

Parasite[1, 2]	Kvichak River			Iliamna Lake	Newhalen River	Lake Clark
	1966	1969		1968	1961	1968
	1.	1.	2.	2.	1.	2.
Number of fish sampled	50	60	152	50	50	50
**Diplostomulum* sp. (spp.?)	--	60(2.0)	67(2.5)	--	--	--
**Diphyllobothrium* spp.	24(1.3)	35(1.2)	66(1.8)	28(1.1)	26(2.0)	2(1.0)
**Triaenophorus crassus*	0	0	3(1.3)	0	20(1.5)	0
Neoechinorhynchus rutili	10(1.2)	2(1.0)	13(1.3)	2(1.0)	0	0
**Philonema oncorhynchi*	100	100	92	100	100	91

[1] * = larval parasites (in fish intermediate host).
[2] Examinations other than in 1969 were taken from fish preserved in 10% Formalin, which restricted accurate counts of *Diplostomulum* and *P. oncorhynchi*.

study (Table 2). Data from Kvichak smolts in 1964 and 1965 (Margolis, 1967) suggest that the incidence of *T. crassus* in Kvichak smolts is generally low, less than 3%, and that the usual intensity is but one or sometimes two plerocercoids per parasitized fish. *T. crassus* has been found regularly in samples from the Wood and Naknek Rivers but only occasionally in those from the Ugashik and Kvichak Rivers (Margolis, 1967).

Metacercariae of *Diplostomulum* occurred in the eye lenses of 60% of the Kvichak smolts in this study but the mean intensities were low, 2.0 to 2.5 parasites per fish. An incidence of 48% (25 fish examined) and an intensity of 2.0 in Kvichak smolts studied in 1956 were tabulated by Margolis (1963).

Margolis (1963) found that 15% of the Kvichak adults returning in 1957 were infected with *Diplostomulum* (mean intensity, 2) and our data (Table 1) closely agree. Thus the incidence but not the intensity of the infections is significantly lower in returning adults than in smolts. Whether this is due to the loss of metacercariae in the lenses of many ocean-dwelling fish, as suggested by Margolis and by Dogiel (1966), or perhaps to disproportionate loss of infected fish as our data hint is conjectural.

The incidence of *Diphyllobothrium* in age 2 Kvichak smolts was 66% from data obtained during this study, but intensities were usually low, with one or two plerocercoids per infected fish. Of the smolts examined from Bristol Bay tributaries in 1957 by Margolis (1963), Kvichak fish ranked second in level of incidence (52%), whereas those from the Egegik River were first with 88% incidence, and those from the Naknek were third with 20% incidence.

Data obtained in this study and provided by Margolis (1963) indicate that nearly all smolts leaving the major rivers of Bristol Bay are infected with larvae of *Philonema oncorhynchi*, but that the intensities vary widely, often exceeding 50 per fish.

It is beyond the scope of this paper to postulate on any effects that the parasites of Kvichak sockeye salmon may have upon the survival of their host. There is ample evidence in the literature that, given certain pre-disposing conditions, direct mortalities from mechanical damage, histopathological changes, and measurable effects upon size and growth rates of parasitized fish do occur. Any factor that results in environmental discrimination, such as the presence of internal and external parasites, would tend to lessen the chances of a fish for survival. The question of whether or not the various parasites occurring in Kvichak sockeye salmon, alone or in combination, cause losses of ecological significance remains to be explored.

POSTSCRIPT

David A. Pennell entered the College of Fisheries of the University of Washington as a graduate student in the fall of 1968. On August 1969, he was involved in a fatal airplane accident while collecting material in the field for his M.S. dissertation on the parasites of sockeye salmon in Bristol Bay, Alaska. This paper is published posthumously in honor of this promising and highly dedicated young man.

Dr. C. Dale Becker undertook to complete the manuscript from a preliminary analysis and report by Mrs. Nora R. Scofield. Supplemental data, collected earlier by Dr. Becker while with the Fisheries Research Institute, have been included in this paper. Assistance and advice were given by Drs. A. K. Sparks and O. A. Mathisen throughout the course of the study.

LITERATURE CITED

ADAMS, J. R.
1969. Migration route of invasive juvenile *Philonema oncorhynchi* (Nematoda: Philometridae) in young salmon. J. Fish. Res. Board Can. 26:941-946.

AKHMEROV, A. KH.
1963. [Helminths as biological indicators of local stocks of Amur anadromous salmon (*Oncorhynchus*).] [In Russian.] Vopr. Ikhtiol. 3:536-555. (Transl. 1968, Fish. Res. Board Can., Transl. Ser. 1048, 24 p.)

BECKER, C. D., AND W. D. BRUNSON.
1967. *Diphyllobothrium* (Cestoda) infections in salmonids from three Washington lakes. J. Wildl. Manage. 31:813-824.

BOYCE, N. P. J.
1969. Parasite fauna of pink salmon (*Oncorhynchus gorbuscha*) of the Bella Coola River, central British Columbia, during their early sea life. J. Fish. Res. Board Can. 26:813-820.

BULLOCK, W. L.
1970. The zoogeography and host relations of the eoacanthocephalan parasites of fishes. *In* S. F. Snieszko (editor), A Symposium on Diseases of Fishes and Shellfishes, p. 161-173. Am. Fish. Soc., Spec. Publ. 5.

BURGNER, R. L., C. J. DICOSTANZO, R. J. ELLIS, G. Y. HARRY, JR., W. L. HARTMAN, O. E. MATHISEN, AND W. F. ROYCE.
1969. Biological studies and estimates of optimum escapements of sockeye salmon in the major river systems in southwestern Alaska. U.S. Fish Wildl. Serv., Fish. Bull. 67:405-459.

CHOQUETTE, L. P. E.
1951. On the nematode genus *Rhabdochona* Railliet, 1916 (Nematoda: Spiruroidea). Can. J. Zool. 29:1-16.

CICHOWLAS, Z.
1961. The life-cycle of *Diplostomum spathaceum* (Rud. 1819) in brackish waters of the Baltic Sea. Acta Parasitol. Pol. 9:33-46.

DOGIEL, V. A.
1966. General parasitology. 3d ed. (Translated by Z. Kabata.) Academic Press, N.Y., 516 p.

DOMBROSKI, E.
1955. Cestode and nematode infection of sockeye smolts from Babine Lake, British Columbia. J. Fish. Res. Board Can. 12:93-96.

EKBAUM, E.
1938. Notes on the occurrence of Acanthocephala in Pacific fishes. I. *Echinorhynchus gadi* (Zoega) Müller in salmon and *E. lageniformis* sp. nov. and *Corynosoma strumosum* (Rudolphi) in two species of flounder. Parasitology 30:267-274.

GINETSINSKAYA, T. A.
1958. [The life cycles of fish helminths and the biology of their larval stages.] *In* V. A. Dogiel, G. K. Petrushevski, and Yu. I. Polyanski (editors), Parasitology of fishes, p. 140-179. (Transl. 1961 by Z. Kabata.) Oliver and Boyd, Lond.

KENNEDY, C. R.
1969. The occurrence of *Eubothrium crassum* (Cestoda: Pseudophyllidea) in salmon *Salmo salar* and trout *S. trutta* of the River Exe. J. Zool. Lond. 157:1-9.

LAWLER, G. H., AND W. B. SCOTT.
1954. Notes on the geographical distribution and the hosts of the cestode genus *Triaenophorus* in North America. J. Fish. Res. Board Can. 11: 884-893.

LINTON, E.
1933. On the occurrence of *Echinorhynchus gadi* in fishes of the Woods Hole region. Trans. Am. Microsc. Soc. 52:32-34.

MAMAEV, YU. L., A. M. PARUKHIN, O. M. BAEVA, AND P. G. OSHMARIN.
1959. [The helminth fauna of Far Eastern salmonids in connection with questions of local stocks and migration routes of these fishes.] [In Russian]. Primorskoe Knizhnoe Izdatel'stvo, Vladivost., 74 p.

MAMAEV, YU. L., AND P. G. OSHMARIN.
1963. [Characteristics of the distribution of some helminths of Far-Eastern salmonids.] [In Russian.] *In* P. G. Oshmarin (editor), Parasitic worms of animals from Primore and the Pacific Ocean, p. 82-113. Akad. Nauk SSSR, Moscow.

MARGOLIS, L.
1958. The occurrence of juvenile *Corynosoma* (Acanthocephala) in Pacific salmon (*Oncorhynchus* spp.). J. Fish. Res. Board Can. 15:983-990.
1963. Parasites as indicators of the geographical origin of sockeye salmon, *Oncorhynchus nerka* (Walbaum), occurring in the North Pacific Ocean and adjacent seas. Int. North Pac. Fish. Comm., Bull. 11:101-156.
1965. Parasites as an auxiliary source of information about the biology of Pacific salmons (genus *Oncorhynchus*). J. Fish. Res. Board Can. 22: 1387-1395.
1967. *Triaenophorus crassus* plerocercoids in sockeye salmon smolts from the Kvichak River system, Alaska. J. Fish. Res. Board Can. 24:893-894.

1970. Nematode diseases of marine fishes. *In* S. F. Snieszko (editor), A Symposium on Diseases of Fishes and Shellfishes, p. 190-208. Am. Fish. Soc., Spec. Publ. 5.

MARGOLIS, L., AND N. P. BOYCE.
1969. Life span, maturation, and growth of two hemiurid trematodes, *Tubulovesicula lindbergi* and *Lecithaster gibbosus*, in Pacific salmon (genus *Oncorhynchus*). J. Fish. Res. Board Can. 26: 893-907.

MERRITT, S. V., AND I. PRATT.
1964. The life history of *Neoechinorhynchus rutili* and its development in the intermediate host (Acanthocephala: Neoechinorhynchidae). J. Parasitol. 50:394-400.

MEYER, M. C.
1966. Evaluation of criteria for the recognition of *Diphyllobothrium* species. Trans. Am. Microsc. Soc. 85:89-99.

MICHAJLOW, W.
1962. Species of the genus *Trianophorus* (Cestoda) and their hosts in various geographical regions. Acta Parasitol. Pol. 10:1-38.

MILLER, R. B.
1952. A review of the Triaenophorus problem in Canadian lakes. Fish Res. Board Can., Bull. 95, 42 p.

PLATZER, E. G., AND J. R. ADAMS.
1967. The life history of a dracunculoid, Philonema oncorhynchi, in Oncorhynchus nerka. Can. J. Zool. 45:31-43.

RAUSCH, R.
1954. Studies on the helminth fauna of Alaska. XXI. Taxonomy, morphological variation, and ecology of *Diphyllobothrium ursi* n. sp. provis. on Kodiak Island. J. Parasitol. 40:540-563.

RAUSCH, R. L., AND D. K. HILLARD.
1970. Studies on the helminth fauna of Alaska. XLIX. The occurrence of *Diphyllobothrium latum* (Linnaeus, 1758) (Cestoda: Diphyllobothriidae) in Alaska, with notes on other species. Can. J. Zool. 48:1201-1219.

SINDERMANN, C. J.
1966. Diseases of marine fishes. Adv. Mar. Biol. 4:1-89.

SMITH, H. D., AND L. MARGOLIS.
1970. Some effects of *Eubothrium salvelini* (Schrank, 1790) on sockeye salmon, *Oncorhynchus nerka* (Walbaum), in Babine Lake, British Columbia. (Abstr.) J. Parasitol. 56(Sect. 2):321-322.

STUNKARD, H. W.
1965. Variation and criteria for generic and specific determination of diphyllobothriid cestodes. J. Helminthol. 39:281-296.

THOMPSON, W. F.
1962. The research program of the Fisheries Research Institute in Bristol Bay, 1945-58. *In* T. S. Y. Koo (editor), Studies of Alaska red salmon, p. 1-36. Univ. Wash. Publ. Fish., New Ser. 1.

VAN CLEAVE, H. J., AND J. E. LYNCH.
1950. The circumpolar distribution of *Neoechinorynchus rutili*, an acanthocephalan parasite of fresh-water fishes. Trans. Am. Microsc. Soc. 69: 156-171.

VIK, R.
1963. Studies of the helminth fauna of Norway. IV. Occurrence and distribution of *Eubothrium crassum* (Bloch, 1779) and *E. salvelini* (Schrank, 1790) (Cestoda) in Norway, with notes on their life cycles. Nytt Mag. Zool. 11:47-73.
1964. The genus *Diphyllobothrium*. An example of the interdependence of systematics and experimental biology. Exp. Parasitol. 15:361-380.

WALKEY, M.
1967. The ecology of *Neoechinorhynchus rutili* Müller. J. Parasitol. 53:795-804.

WATSON, N. H. F., AND G. H. LAWLER.
1965. Natural infections of cyclopid copepods with procercoids of *Triaenophorus* spp. J. Fish. Res. Board Can. 22:1335-1343.

WILLIAMS, H. H.
1968. The taxonomy, ecology and host-specificity of some Phyllobothriidae (Cestoda: Tetraphyllidea), a critical revision of *Phyllobothrium* Beneden, 1849 and comments on some allied genera. Philos. R. Soc. Lond., Ser. B 253:231-307.

ZHUKOV, E. V.
1960. [Endoparasitic helminths of fishes from the Japan Sea and South Kurile shallows.] [In Russian, English summary.] Tr. Zool. Inst. Akad. Nauk SSSR 28:1-146.